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Hiding in the bushes for 110 years: rediscovery of an iconic Angolan gecko (*Afrogecko ansorgii* Boulenger, 1907, Sauria: Gekkonidae)

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***Abstract.*—Boulenger (1907) described a new gecko '*Phyllodactylus*' *ansorgii* based on two adult females from 'Maconjo, Benguella, Angola,' but subsequent taxonomic reviews of leaf-toed geckos ascribed southern African lineages to new genera and this species has since been tentatively placed under '*Afrogecko*.' For over 110 years the type locality remained a mystery, and the gecko became a lost icon of Angolan herpetology. Early searches for the gecko were confounded by misinterpretation of the type locality 'Maconjo,' which it is now evident was confused with a toponym that is a well-known historical locality. Following the discovery of new material in coastal Benguela, an examination of historical documents and cartographic material allowed the original collecting area for the type material to be identified. Specific surveys in this area resulted in the collection of topotypic material and the recording of behavioral observations and notes on the ecology of the species. *Afrogecko ansorgii* is a slender, gracile, and arboreal gecko that inhabits small bushy trees, particularly blackthorn (*Senegalia mellifera* subsp. *detinens*), in the arid coastal scrubland of the Benguela coastal region. All *A. ansorgii* have been found in or nearby blackthorn in which the activity of termites (Kalotermitidae) has created hollow stems in which the geckos shelter. The type locality for *Phyllodactylus* (= *Afrogecko*) *ansorgii* Boulenger, 1907 and *Mabuia* (= *Trachylepis*) *laevis* Boulenger, 1907, both described at the same time from 'Maconjo, Benguella' is accordingly restricted, and topotypic material for the latter species was also obtained.**

Key Words. Ansorge, blackthorn, Kaokoveld, Maconjo, Reptilia, type locality, *Trachylepis laevis*

***Resumo.*—Boulenger (1907) descreveu a nova osga '*Phyllodactylus*' *ansorgii* a partir de duas fêmeas oriundas de 'Maconjo, Benguella, Angola,' mas subsequentes revisões taxonómicas das osgas-de-dedos-de-folha fez corrresponder a novos géneros as linhagens da África austral e desde então esta espécie tem sido tentativamente incluída em 'Afrogecko.' Durante mais de 110 anos a localidade típica permaneceu um mistério, e a osga tornou-se um ícone perdido da herpetologia Angolana. Buscas iniciais pela osga ficaram baralhadas devido a uma má interpretação da localidade típica 'Maconjo,' que é hoje evidente ter sido confundida com um topónimo que é uma localidade histórica bem conhecida. Após a descoberta de novo material na região costeira de Benguela, a despistagem de documentos históricos e material cartográfico permitiu identificar a área de colheita original do material típico. Levantamentos específicos nesta área resultaram na colheita de material topotípico e no registo de observações comportamentais e notas sobre a ecologia da espécie. O *Afrogecko ansorgii* é uma osga delgada, delicada e arborícola que habita pequenas árvores de porte arbustivo, particularmente espinheiras (*Senegalia mellifera* subsp. *detinens*), nas estepes áridas arbustivas da região costeira de Benguela. Todos os *A. ansorgii* foram encontrados nestas espinheiras ou na sua vizinhança, e onde a actividade de térmitas (Kalotermitidae) gerou talos ocos onde as osgas se abrigam. A localidade típica para o *Phyllodactylus* (= *Afrogecko*) *ansorgii* Boulenger 1907 e para o *Mabuia* (= *Trachylepis*) *laevis* Boulenger 1907, ambos descritos na mesma altura para 'Maconjo, Benguella', é desta forma restringida, e material topotípico da última espécie foi também obtido.**

Palavras-chave: Reptilia, localidade típica, Maconjo, Ansorge, espinheira, Kaokoveld, *Trachylepis laevis*

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Introduction

The biodiversity of Angola, and particularly that of the herpetofauna, is acknowledged to be inadequately known (Branch 2016; Huntley and Ferrand 2019). This was not always the case, and like many countries in Africa the early phase of colonial exploration and settlement resulted in the discovery of numerous novel animals. For almost 50 years (1866–1915) these collections were sent to European museums for study and description, and they stimulated much scientific interest. Early studies on the Angolan herpetofauna were numerous, particularly those of José Vicente Barbosa du Bocage, the father of Angolan herpetology. His monographic *Herpétologie d'Angola et du Congo* (Bocage 1895) remained for over a century the definitive synthesis of the country's herpetofauna, until the recent publication of a historic herpetological atlas (Marques et al. 2018). Currently, studies on the herpetofauna of Angola are entering a new phase following the closure of protracted hostilities at the end of the colonial era. Recent field surveys (e.g., Huntley 2009; Ernst et al. 2014; Huntley and Francisco 2015; Ceríaco et al. 2016, 2018; Conradie et al. 2016) have uncovered new species of amphibians (Conradie et al. 2012a, 2013; Ceríaco et al. 2018) and reptiles (Conradie et al. 2012b; Stanley et al. 2016). However, a number of important historical species described during the colonial period still remain known from only their original description, e.g., *Sepsina copei* Bocage, 1866 and *Cordylus angolensis* (Bocage 1895), or only a few subsequent specimens, e.g., *Monopeltis luandae* Gans 1976 (Branch et al. 2018), *Psammophis ansorgii* Boulenger 1905, and *Psammophylax ocellatus* Bocage 1873 (Branch et al. 2019a). Tragically, much of the historical material studied by Bocage, including almost all of his type material, was lost in the fire that destroyed the Museu Bocage collections in 1978.

Perhaps the most iconic of the 'lost' Angolan species is Ansorge's Leaf-toed Gecko, which was described by Boulenger (1907) as *Phyllodactylus ansorgii*, over 110 years ago. Leaf-toed geckos have a globally wide-ranging distribution and all of them used to be included within *Phyllodactylus* until a comprehensive review performed by Bauer (1997) ascribed the southern African species to three new genera. The genus *Afrogecko* initially included two species found in South Africa, *A. porphyreus*, and *A. swartbergensis*, and two Angolan leaf-toed geckos, *A. plumicaudus* and *A. ansorgii* (Bauer 1997; Haacke 2008). However, more recent phylogenetic studies revealed deeply independent evolutionary histories among these lineages, leading *A. swartgergensis* and *A. plumicaudus* to be transferred to the new monotypic genera *Ramigekko* and *Kolekanos*, respectively, while due to the lack of available material *ansorgii* was provisionally maintained within *Afrogecko* (Heinicke et al. 2014).

The species description was based on two female specimens from Maconjo, Benguella (now Benguela) collected by Dr. W.J. Ansorge on one of his Angolan journeys, between 1903 and 1906, and the types, BMNH 1946.8.24.52–53, were deposited in the Natural History Museum London (United Kingdom). The exact locality of Ansorge's Maconjo has caused confusion, and erroneous interpretation of its whereabouts probably delayed the species' rediscovery. Moreover, the species is now known to live in an unusual habitat, and this may have also led to it being overlooked. Crawford-Cabral and Mesquitela (1989) summarized all known localities for Angolan terrestrial vertebrates and considered Maconjo a variant spelling of Maconge, an old farm situated in Namibe Province, formerly Mossamedes (= Moçâmedes) District (15°01'S, 13°12'E, 700 m asl). Maconjo, Mossamedes features as a collecting locality for reptiles in the 19th century for the famous Portuguese collector José de Anchieta (de Andrade 1985), and in his monograph Bocage (1895) recorded numerous reptiles from Maconjo, Mossamedes, including: the terrapin *Pelomedusa galeata* (= *P. subrufa*); the lacertids *Nucras tessellata* and *Eremias lugubris* (= *Heliobolus lugubris*); the rupicolous skink *Mabuia chimbana* (= *Trachylepis chimbana*); the python *Python natalensis*; the snakes *Prosymna frontalis* (= *P. angolensis*, *fide* Broadley 1980), *Psammophylax nototaenia* (= *Hemirhaggheris viperina*, *fide* Broadley 2000), *Psammophis sibilans* (= *P. subtaeniatus*), *Elapsoidea guentheri* var. *semiannulata* (= *E. s. semiannulata*), and *Causus resimus*. Many of these have been subsequently recorded in the region (data not shown).

A farm and stream at the base of the Humpata plateau near Leba Pass are called Maconjo on old maps and lie in the vicinity of the old Portuguese fort of Capangombe, which dates from the mid-nineteenth century and marks the route for some of the earliest inland incursions of colonists in southern Angola. This locality was then included in the District of Mossamedes. However, Boulenger referred the gecko's type locality to 'Maconjo, Benguella,' placing it in Benguela instead of Mossamedes District. This suggests either that it was ascribed by Ansorge to the wrong district, or that there could exist two different sites bearing the name Maconjo. It should be noted that mistaking Mossamedes for Benguela would have been unlikely in the early 20th century, when both districts were well established and had been for some time. They have also remained as separate administrative entities ever since. Yet this incongruence seems to have gone unnoticed, and it appears that most subsequent researchers have considered there was only one Maconjo, and the references to different provinces, Mossamedes (= Namibe) or Benguela, were either ignored or taken as synonyms (Bauer et al. 1997; Heinicke et al. 2014; Ceríaco et al. 2016; Uetz et al. 2018). The accepted wisdom that there was only one Maconjo, and that it was situated below the escarpment in the current Namibe Province, resulted in numerous unsuccessful searches for the gecko around Capangombe by various researchers from 1974 to 2016. More recently, Maconjo was tentatively synonymized with another well-known collecting site in southwestern Angola 'Fazenda Mucungo' (Marques et al. 2018), however, no further details were provided to justify the new locality. Mucungo also lies on the coastal plain of Namibe and therefore cannot resolve the geographical discrepancies.

Another species from 'Maconjo' that Boulenger (1907) described from the same Ansorge collection

was the small rupicolous skink *Mabuia* (= *Trachylepis*) *laevis*, commonly called the Angolan Blue-tailed Skink (*T. laevis*). It is rupicolous, sheltering in thin cracks in hard, fractured rocks and has numerous morphological adaptations to this habitat (Paluh and Bauer 2017). Despite its conspicuous coloration, the species has only rarely been collected in Angola after the original description (Boulenger 1907). Laurent (1964) recorded a male from Munhino, 50 km W of Lubango, and Hellmich (1957) reported a problematic specimen from Piri-Dembos (= Piri) that should be treated with caution (Laurent 1964; Ceríaco et al. 2016). The Angolan Blue-tailed Skink was recently recorded from granite outcrops 50 km east of Namibe (W.R. Branch, pers. comm.), and just north of Tambor near Iona National Park (Ceríaco et al. 2016), and additional material has been collected in northern Namibe Province, at Chapéu Armado, Serra da Neve, and Lola by the authors of the current study. Still, the most significant collections of *T. laevis* were made by Wulf Haacke during an expedition to southwestern Angola in 1971, when he collected 18 specimens from Tambor and other localities in Namibe Province (all deposited in the Ditsong Natural History Museum, Pretoria, South Africa). In addition, and importantly, he collected the first records since Ansorge from Benguela Province, with material from 35 km south of Dombe Grande and 53 km south of Benguela.

Until now, no additional material for *A. ansorgii* had ever been collected, despite searches by experienced herpetologists in the 1970s and after 2009. In this paper we report on finding the species and obtaining new material that includes the first male specimens. The type locality is here confidently restricted, and topotypic material was collected for both *A. ansorgii* and *T. laevis*. In addition, by collecting the gecko on a second site, we extend its known range by about 100 km. Behavioral and habitat observations were also recorded, and provide useful insights into their unique ecological requirements.

Materials and Methods

To investigate local toponyms and locate the type locality, historical cartographic material was thoroughly examined and, in the absence of available diaries for Dr. Ansorge's Angolan journeys, we consulted a remarkable manuscript by the American ornithologist James Chapin which provides a detailed summary of Ansorge's itineraries in Angola (Chapin, undated).

After first encountering *A. ansorgii*, we conducted a series of additional field trips in search of the gecko between November 2016 and June 2018, to five different sites, including the restricted type locality and additional locations where we looked for their presence. The surveys included mostly nocturnal searches, and daytime habitat observations. A total of 23 specimens of *A. ansorgii* were collected in two sites, including the restricted type locality. All specimens were photographed in life, and subsequently preserved in formalin. Collected specimens were deposited at Port Elizabeth Museum (PEM R23907–23916), at ISCED – *Instituto Superior de Ciências da Educação da Huíla* (NB603–605; NB822–826) and at Kissama Foundation (KFH0007–0010). Additionally, behavioral observations were also recorded by locating the geckos at night with flashlights and observing their foraging habits, and by confirming their daytime shelters. Reptile species lists were compiled for each site visited, and topotypic material was also secured for *T. laevis*, with one specimen collected and deposited at Kissama Foundation collection (FKH0018).

Results

Type locality: From Chapin's summary it is apparent that Ansorge visited 'Makonjo, Benguella' on 7 July 1904. Chapin used the spelling 'Makonjo' instead of following Boulenger's 'Maconjo,' but the use of a 'k' or 'c' is often interchangeable when applied to Angolan toponymy. To avoid continued confusion with toponyms we hereafter keep the spelling as Maconjo and add the district/province name when relevant. Ansorge left the locality of 'Huxe, Benguella' (= Uche, 12°44'S, 13°21'E, 250 m asl) on the previous day on his way to Benguela's sandpits and the town of Catengue (13°02'S, 13°44'E, 550 m asl), which he reached on 11 July 1904. This route, depicted on a map included in the manuscript, places the locality of Maconjo clearly in Benguela as opposed to Namibe's coastal plain, and within a few days travel on foot from Benguela town. In addition, there are no other records of localities of similar spelling in the manuscript, and no suggestion that Ansorge ever visited Capangombe region. Moreover, based on Chapin's document it appears that Ansorge never descended the escarpment from the Humpata plateau, and although he referred to his 1906 route south of Caconda as being in Mossamedes District, Chapin failed to recognize the then newly created Huíla District. As a result, there is no evidence to suggest that Ansorge even collected in the former Mossamedes District as it was defined in his time, and which broadly corresponds to the current Namibe Province.

Comparing Chapin's notes with cartographic material allowed the reconstruction of Ansorge's probable route (Fig. 1) and the identification along it of a region by the name of 'Conjo' (12°53'S, 13°24'E) in Benguela Province. This area, approximately 20 km south of Uche and on the route towards Catengue, lies between 300 and 450 m asl, and includes two small north-flowing dry sandy streams named respectively as 'Conjo' and 'Conjo Pequeno,' both tributaries to another ephemeral stream named 'Cocumba.' The region is in Benguela's coastal plain and would be realistically within one-day's reach from Uche on foot, and enroute to Catengue, making it extremely likely that it corresponds to the true type locality of 'Maconjo, Benguela' as recorded by Ansorge (in Boulenger 1907). Interestingly, in the local language Conjo means spoor and the prefix 'Ma-' is commonly used to signify plurality, so the toponymy Maconjo can be appropriately interpreted as 'the site of various Conjos' or 'site of many spoor.'

On the basis of Chapin's notes and cartographic material we here restrict the type locality of *Phyllodactylus* (= *Afrogecko*) *ansorgii* and *Mabuia* (= *Trachylepis*) *laevis*, both described by Boulenger (1907) from 'Maconjo, Benguella,' to the vicinity of the streams Conjo, Conjo Pequeno, and Cocumba (12°52'S, 13°21'E, 355 m asl),

Fig. 1. Travel routes in Angola by Dr. Ansorge between 1904 and 1906, as per Chapin's manuscript. Former district (broadly corresponding to current provinces) borders are shown, as well as collecting sites and other relevant localities.

20 km south of Uche, Benguela Province, Angola (Fig. 1). Both species, *Afrogecko ansorgii* and *Trachylepis laevis*, were collected at this site (see below).

Rediscovery: The gecko was first rediscovered 135 km southwest of Benguela town on 12 November 2016. The site is located about three km from the Lucira-Benguela road, at the head of a valley leading down to Cape Sta Maria, Benguela Province (13°31'S, 12°38'E, 288 m asl). The locality is ca. 185 km northwest of Maconjo, Namibe, and ca. 100 km southwest of the type locality in Benguela Province (Fig. 1). A total of 10 specimens were collected at night whilst foraging in the branches of thorny bushes (Fig. 2), mainly of blackthorn *Senegalia mellifera detinens*. Subsequently, three additional specimens were collected, and nine others observed in the same habitat and under similar circumstances, at two other nearby sites surveyed five km and three km to the northwest, on 12–13 July 2017 and 11–12 August 2017, respectively. Most specimens were located at night on bushes situated at the base or mid-slopes of granitic hills, and although a few were observed in various species of small trees, the majority were found among the spiny branches of blackthorn bushes. One specimen was found during the day sheltering inside a hollow blackthorn branch (Fig. 3A).

After the cartographic identification of the potentially true type locality, specific visits to the Conjo area to search for geckos were made on 25–26 November 2017 and 5 December 2017. The region surveyed was located approximately half-way between the towns of Benguela (35 km) and Catengue (47 km) and five km south of the small village of Talamajamba. As it shared some features with sites at Sta Maria, although lacking in rocky habitat suitable for *Trachylepis laevis*, we first focused on a site located on a sand road that crosses the Cocumba dry stream and runs a few hundred meters parallel to the east of Conjo Pequeno (12°54'3S, 13°24'E, 395 m asl). The searches resulted in our obtaining topotypic material and further observations. Broadening the search, additional visits on 12–13 March 2018 and 5 June 2018, focused on an area around three isolated granite outcrops present along the stream Cocumba and a mere 500 m west of the confluence with stream Conjo (12°52'S, 13°21'E, 355 m asl). Although the Cocumba is a dry stream on a semi-desert environment, local pastoralists have long dug artisanal wells to gain access to water on the river bed at the base of the granite outcrops. The presence of these wells on the confluence of Conjo and Cocumba streams offers a realistic scenario for the site 'Maconjo' to have been used as a stopover locality between Benguela and Catengue by Ansorge in 1904. Here, additional specimens of *A. ansorgii* were found in nearby bushes, and a specimen of *T. laevis* was collected in the granite outcrops, constituting the first topotypic material for this species.

At Maconjo, a total of 10 specimens of *A. ansorgii* were collected and 14 additional individuals were observed foraging at night in bushes over the four visits, mostly found in *Senegalia mellifera detinens*, but also in *Terminalia prunioides*, *Commiphora* cf. *africana*, and *Salvadora persica*, and once on a dry grass stem. Most geckos were spotted in the early evening (approximately between 19h00 and 21h00) in small branches 1–2 m above ground. One specimen was observed partially exiting a hollow blackthorn branch shortly after sunset, as exemplified in a photograph (Fig. 3B).

Three additional coastal sites (Fig. 1) were also surveyed in search of the geckos, one was an intermediate location between Maconjo and Sta Maria, at Chimalavera Regional Park (12°50'S, 13°10'E, 255 m asl), on a sandy plateau over an east-facing limestone ridge, Benguela Province; another ca. 35 km south of Maconjo and near the Coporolo River (13°12'S, 13°25'E, 380 m asl); and one further south at 17 km W of Chicambi Village, on sandy flats with a granite ridge, in Namibe Province (13°55'S, 12°41'E, 531 m asl). In these sites the habitat was similar to that at Cape Sta Maria, with numerous *Senegalia mellifera detinens* bushes on sandy soil and with adjacent rock outcrops. However, in all these three cases the blackthorn bushes lacked hollow branches and no geckos were observed during nocturnal searches.

Habitat observations: On the vegetation map of Angola, Barbosa (1970) defines a very extensive region as semi-desert coastal steppe, starting as a narrow coastal strip around 11° south, then becoming broader inland towards the southern border with Namibia. However, this is a very wide and rough classification and includes a transition from dry spiny savannahs dominated by acacias (*Senegalia* spp.) to mopane woodlands characterized

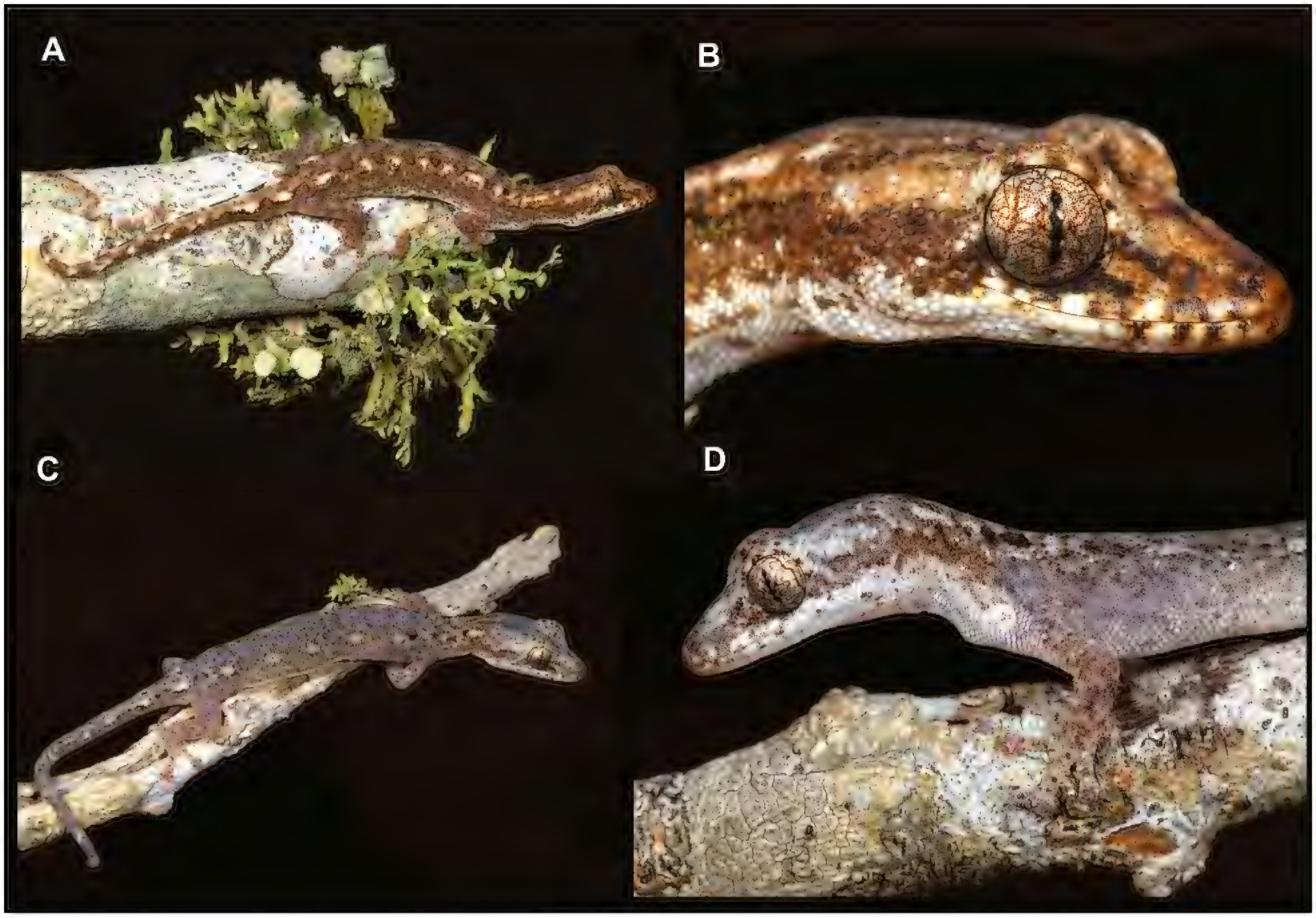

Fig. 2. *Afrogecko ansorgii*: adult male, PEM R23907 (in life). **(A)** Whole body on small branch of *Senegalia mellifera detinens* with epiphytic lichen. **(B)** Close up of head of same adult male. **(C)** *Afrogecko ansorgii*: adult female, PEM R23912 (in life) on small branch of *Senegalia mellifera detinens.* **(D)** Close up of head of same adult female. Note elongate, subcylindrical body, relatively short cylindrical tail that is shorter than SVL and partially prehensile, long toes with expanded terminal scansors, predominantly dark brown dorsal coloration, and dorsolateral series of irregular pale blotches that extend on to the tail.

by the dominance of *Colophospermum mopane*. Still, he refers to the arid regions near Benguela as being characterized by an abundance of *Senegalia mellifera detinens*, *Senegalia* spp., *Salvadora persica*, *Euphorbia* spp., and *Boscia* spp. (Barbosa 1970) which likely correspond to the more relevant areas for Ansorge's Gecko.

At Maconjo, Benguela, the restricted type locality, the terrain is relatively flat, with sandy soils, irregularly interspersed with small granitic rocks, and with a few isolated granite outcrops at the Cocumba stream (Fig. 4A). The vegetation was relatively dense and diverse, the trees often in close proximity or touching, but with low canopies and not growing larger than the size of a bush (Fig. 4B). The dominant tree/bush species were *Senegalia mellifera detinens* and *Terminalia prunioides*, but other species also found to be common were *Commiphora* cf. *africana*, *Boscia microphylla*, *Vachellia reficiens*, and *Salvadora persica*. Succulents were also recorded, notably the conspicuous *Aloe littoralis*, plus a few *Hoodia* cf. *parviflora* and the invasive *Opuntia ficus-indica*.

The Sta Maria site is situated at a slightly lower elevation, being closer to the coast and further south than the type locality, and in a more arid coastal environment. It possibly receives lower rainfall, but this may be compensated for by the higher incidence of coastal fog which is a feature of the whole Namib Desert coastline (Cermak 2012). The effect of regular fogs, which may extend well inland, is evident in the local abundance of lichens that often cover the branches of bushes (Figs. 2A, 4C). At this locality the vegetation was much sparser than at Maconjo, Benguela, particularly in the sandy valleys, but the topography was often much more varied with large granite boulders and steep granitic hills (Fig. 4D). *Senegalia mellifera detinens* was the most abundant tree, while other common species recorded were *Salvadora persica*, *Commiphora multijuga*, *Phaeoptilum spinosum*, and *Terminalia prunioides*.

A striking find that appears positively linked with the occurrence of the gecko is the existence in both sites of abundant hollow branches in *Senegalia mellifera detinens* caused by the activity of termites (Kalotermitidae) [Fig. 5]. By eating the heartwood of dead branches and leaving the outer wood and bark intact, the termites hollow out branches, making small exit holes at the branching nodes. This activity creates ideal daytime shelters for *Afrogecko ansorgii*, with multiple entry and exit points. These hollow branches subsequently break off and accumulate below the tree, where they may still be used as refugia by the geckos.

Table 1. Variation observed for *Afrogecko ansorgii*, comparing the type series from Maconjo, with new series obtained in Maconjo and Sta Maria. Continuous measurements in mm (mean and range) for TL= total length, SVL= snout-vent length and Tail. Meristic and qualitative variation (median and range) is given for number of precloacal pores and cloacal spurs.

	TL	SVL	Tail	Pores	Spurs
Type Series – Maconjo					
Females (n=2)	7–5	45	30	0	na
New Series – Maconjo					
Females (n=5)*	75.1	43.9	31.3	0	1
	(71.4–79.0)	(41.3–45.8)	(30.1–33.2)	0	1
Males (n=4)	65	38.2	26.8	8	2
	(57.8–68.8)	(34.4–40.6)	23.4–29.0)	8–9	2
Juvenile Female (n=1)	68	38.6	29.4	0	1
New series – Sta Maria					
Females (n=5)**	63.3	39.4	23.8	0	0
	(56.2–69.3)	(34.7–42.9)	(22.0–26.4)	0	0
Males (n=6)**	60	35.7	24.2	9	1
	(53.2–63.5)	(34.4–38.0)	(18.8–27.5)	7–9	1–2
Juvenile Female (n=1)	54.4	32.3	22.1	0	0

* For Tail and TL measurements n=3 due to truncated tails; ** For Tail and TL measurements n=4 due to truncated tails.

Natural history: The geckos were mostly first seen lying flat or moving slowly on thin branches in the early hours of the evening. Nevertheless, they proved to be agile when disturbed, often running along the branches or even jumping between twigs. The tail was kept low most of the time and appeared to be semi-prehensile. Based on our observations they retreat to safety inside the hollow branches of *Senegalia mellifera detinens* during the day, and emerge soon after dark to forage, mostly on thin branches but not restricted to the acacias. They likely avoid the ground and no specimen was found walking on soil or rock, but their agility allows them to move across neighboring trees, particularly where there is a high density of bushes, as at Maconjo, or where canopy contact is facilitated by uneven and steep slopes as in Sta Maria. A nocturnal arboreal foraging behavior has also been recorded for another Angolan endemic gecko, the possibly closely related species *Kolekanos plumicaudus*, although the latter retreats into rock crevices for shelter (Agarwal et al. 2017).

The geckos probably prey on small insects found on the outer branches of bushes, and it is possible that they also feed on alates of the same termites that provide them with the sheltering habitat, although this could not be confirmed as gut content analyses were not performed. The vast hollow branches with narrow entrances likely preclude many snakes from preying on adults and eggs. In any case, one specimen of *Psammophis leopardinus* was collected, while actively moving at night among the outer branches of a blackthorn bush at Maconjo (Fig. 6A), strongly suggesting that it was hunting *A. ansorgii*.

At both localities the gecko *Hemidactylus* cf.

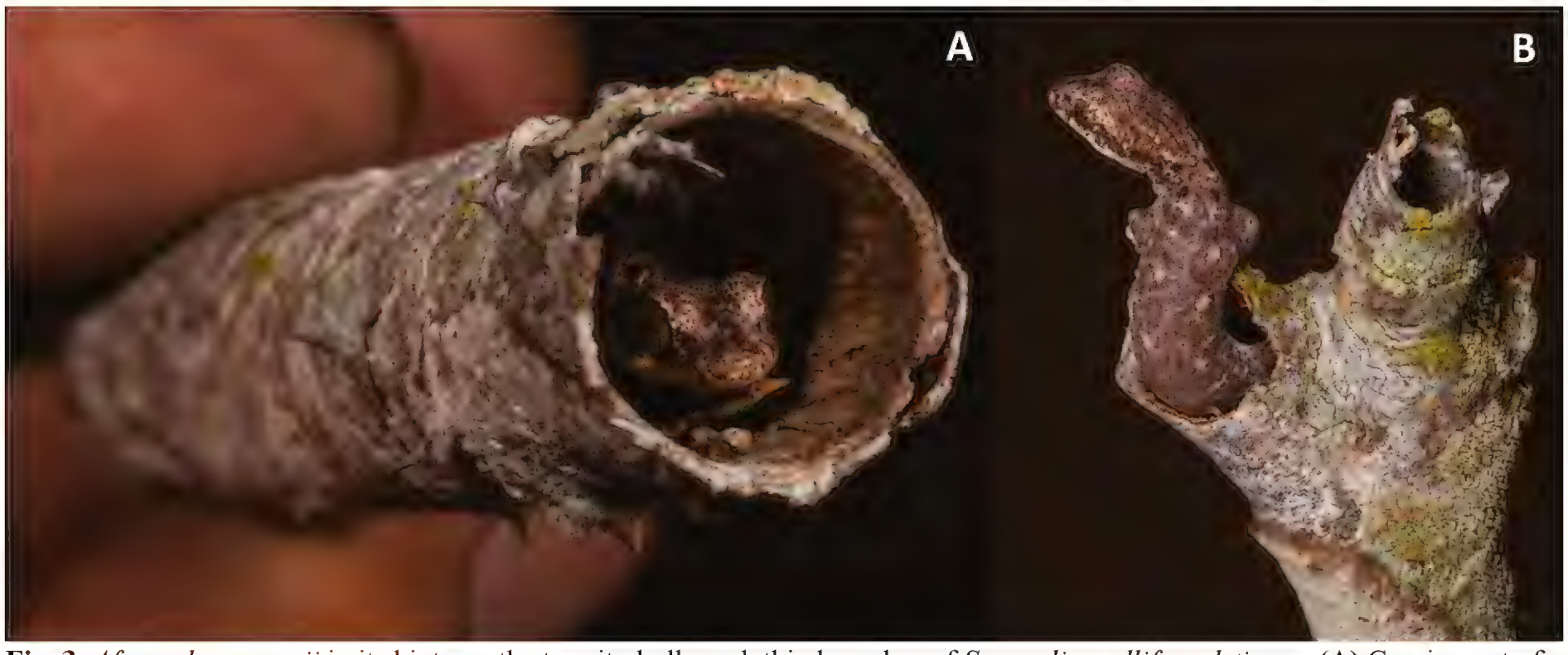

Fig. 3. *Afrogecko ansorgii* in its biotope, the termite-hollowed, thin branches of *Senegalia mellifera detinens*. **(A)** Coming out of a hollow blackthorn twig. **(B)** Specimen caught trapped inside a blackthorn branch.

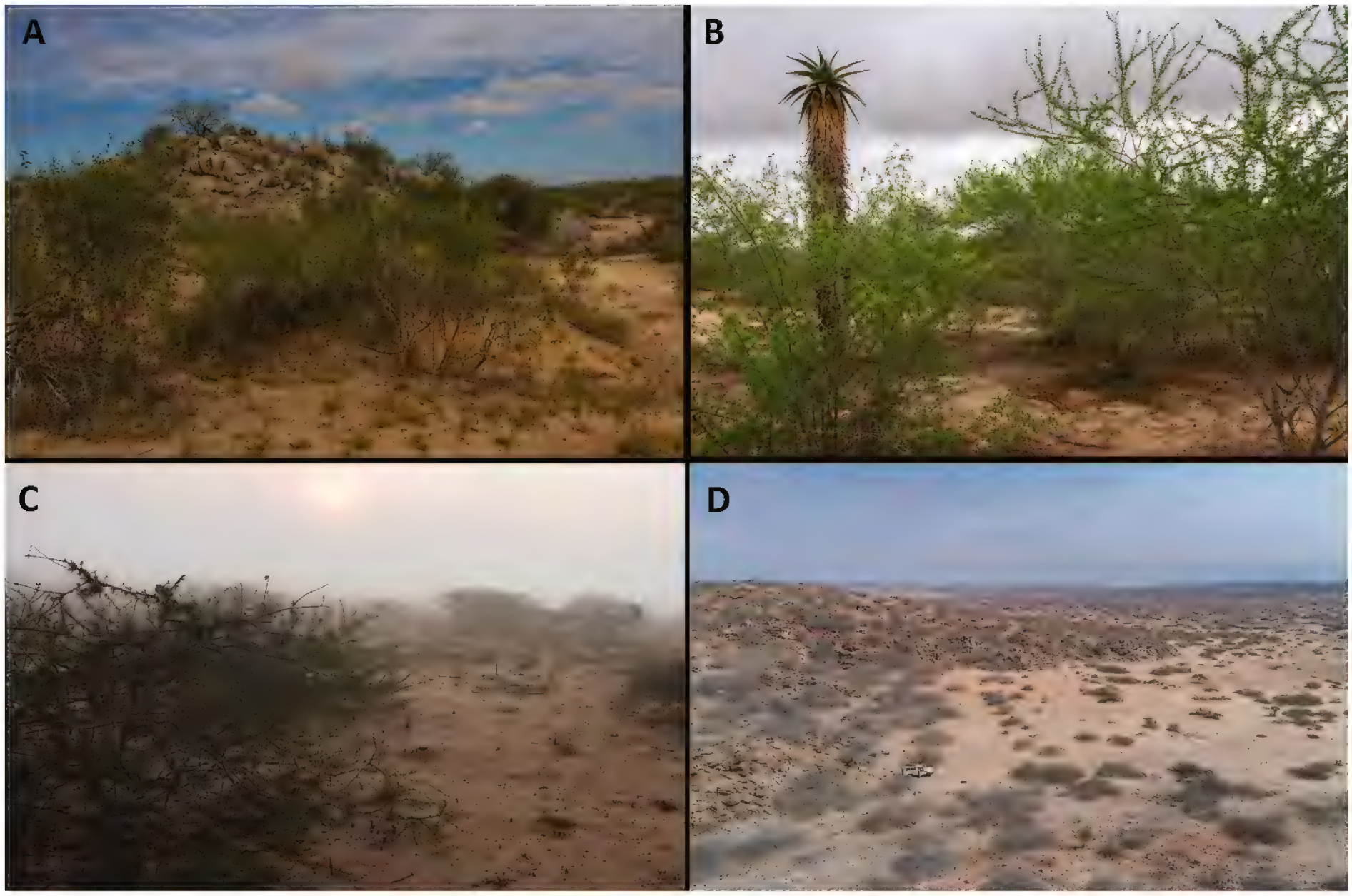

Fig. 4. Habitat of *Afrogecko ansorgii*. **(A)** Isolated granite outcrop beside the dry Cocumba stream near its confluence with Conjo Stream (12°52'S, 13°21'E, 355 m asl), the correct site of Boulenger's type locality 'Maconjo' for *Phyllodactylus ansorgii* and *Mabouia laevis*. **(B)** Spiny savanna of *Senegalia mellifera detinens* with *Terminalia prunioides* and *Aloe littoralis* at the type locality. **(C)** Scattered blackthorn bushes subject to thick morning fog and covered with lichen within which *Afrogecko ansorgii* was rediscovered. **(D)** Aerial view of dry spiny savannah at the head of a valley leading down to Cape Sta Maria, Benguela Province (13°31'S, 12°38'E, 288 m asl).

longicephalus was collected in syntopy in the same bushes, although usually foraging on thicker branches and closer to the ground. Other rupicolous reptile species on the surrounding rocks on both sites included *Pachydactylus caraculicus*, *Chondrodactylus fitzsimonsi, C. pullitzerae*, *Trachylepis laevis* (Fig. 6B), *T. sulcata ansorgii*, *Agama planiceps*, the diurnal *Rhoptropus* cf. *benguellensis* and *R.* cf. *barnardi*; and the terrestrial species *Pachydactylus punctatus, Trachylepis acutilabris,* and *Pedioplanis benguellensis*. Species found in Sta Maria but not recorded at Maconjo were *Afroedura* cf. *bogerti*, *Pachydactylus* cf. *oreophilus*, *Cordylus namakuiyus,* and *Hemirhagerrhis viperina*, while *Matobosaurus maltzahni, Agama anchietae*, *Trachylepis binotata,* and *Psammophis leopardinus* were found at Maconjo but not at Sta Maria. These records include northern extension ranges of roughly 200 km or more for three gekkonids, *Chondrodactylus fitzsimonsi*, *Pachydactylus caraculicus,* and *Rhoptropus* cf. *barnardi*, and for the endemic and recently described *Cordylus namakuiyus* (Stanley et al. 2016).

Distribution range: So far, the gecko has only been found in the two referred localities of Maconjo and Cape Sta Maria, spanning across over 100 km on Benguela's coastal plain. It is likely that the species has a wider distribution range, where it may be locally common but irregularly distributed, and dependent on very particular habitat requirements in association with *Senegalia mellifera detinens* and the kalotermitid termites.

New series and morphological variation: The new material obtained in both localities is consistent with the original description of *Afrogecko ansorgii*. The more slender form and the enlarged precloacal scales well distinguish this species from *A. porphyreus* (Daudin 1802), while the larger size, presence of femoral spurs and a slender semi-prehensile versus a broad flattened tail clearly separates it from the other Angolan endemic Leaf-toed Gecko *Kolekanos plumicaudus* (Haacke 2008). Boulenger's description, based on one of two available adult females, is terse but conforms to that of the era and is given below, while some measurements, including the new series, are presented in Table 1. Male specimens were obtained for the first time, allowing comparisons between sexes and localities. A detailed re-description of *A. ansorgii* is being prepared, which will also explore phylogenetic relationships and include a taxonomic review (data not shown). Original description of *Afrogecko ansorgii* (Boulenger 1907):

> *Head rather small, oviform, much longer than broad; snout not longer than the distance between the eye and the ear opening, which is small and oval. Body*

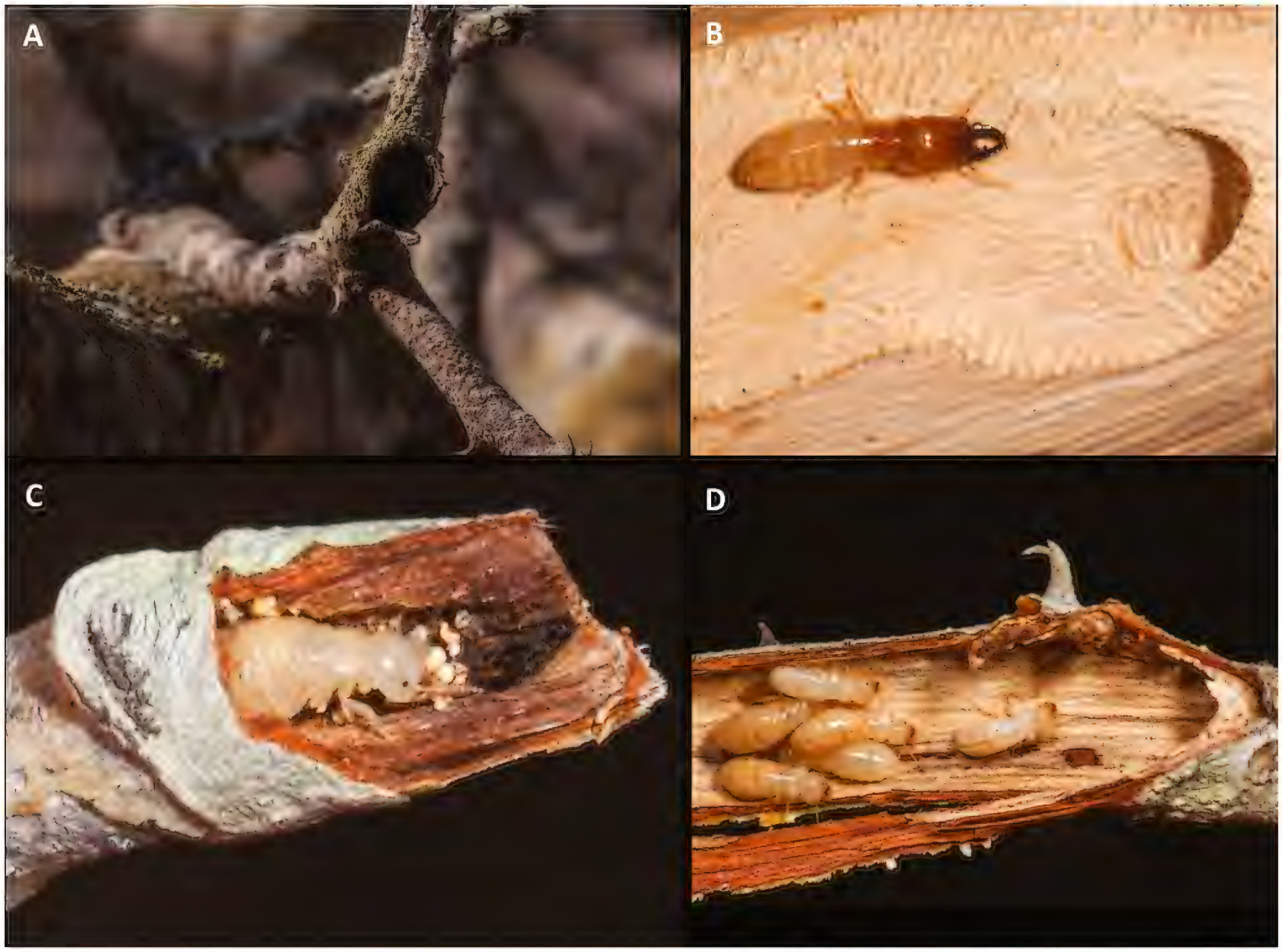

Fig. 5. Kalotermitid termites active on blackthorn bushes at type locality. **(A)** Hollow branch in tree. **(B)** Termite soldier and evidence of wood excavation. **(C)** Termite and eggs inside branch. **(D)** Workers active inside hollow branch.

very elongate; limbs moderate. Digits moderately depressed, with large, subtrapezoid terminal expansions; eight lamellae under the fourth toe. Head and body covered with uniform, smooth, flattened granules, which are larger on the snout and on the belly. Rostral twice as broad as deep, without cleft above; symphysial small, a little longer than broad; ten upper and as many lower labials; rostral and first upper labial entering the nostril; no chin-shields. Tail cylindrical, tapering, covered with uniform, small, quadrangular, smooth scales. A curved transverse series of eight or nine enlarged praeanal scales (indicating praeanal pores in the male?). Pale greyish brown above, with a series of large whitish spots along each side of the back; a dark streak on each side of the head and neck, passing through the eye; upper lip and lower parts white, with small brown spots.

Two females collected in the type locality were gravid with two eggs (Fig. 7A). Male specimens are noticeably smaller than females in snout-vent and total length, with the difference being more pronounced at the type locality. As predicted by Boulenger, males have 7–9 precloacal pores (Fig. 7B), corresponding to the enlarged scales found on females (Fig. 7C). Of note are the differences found between the series obtained at Maconjo and Sta Maria. Specimens from Maconjo proved to be consistently larger in size and overall measurements, with females from Sta. Maria of approximately similar size as males from Maconjo (Table 1). Also striking is the presence of more cloacal spurs in the series from the type locality. Although not mentioned in the type description, we found one cloacal spur in females from Maconjo (Fig. 7A), and two spurs in males from same locality (Fig. 7B). On the other hand, females from Sta Maria showed no cloacal spurs, while at the same site all males but one had one single spur (Table 1).

Discussion

The traditional reliance of gekkonid systematics on digital morphology is often reflected in the generic names, with the Leaf-toed Geckos, *Phyllodactylus* being one of numerous examples. Until the end of the 20th century, gecko species assigned to *Phyllodactylus* had a patchy distribution, spread across five continents. Increasing awareness of both the antiquity of gekkotan lineages (Kluge 1987; Conrad and Norell 2007), of the taxonomic confusion generated by their conflicting conservative and sometimes convergent morphologies (Bauer et al. 1997; Gamble et al. 2012), and of the development and application of molecular phylogenetic studies (Han et al. 2004; Wiens et al. 2012), have resulted in a true understanding of gecko antiquity and diversity. Taxonomic re-arrangements to reflect this evolution and

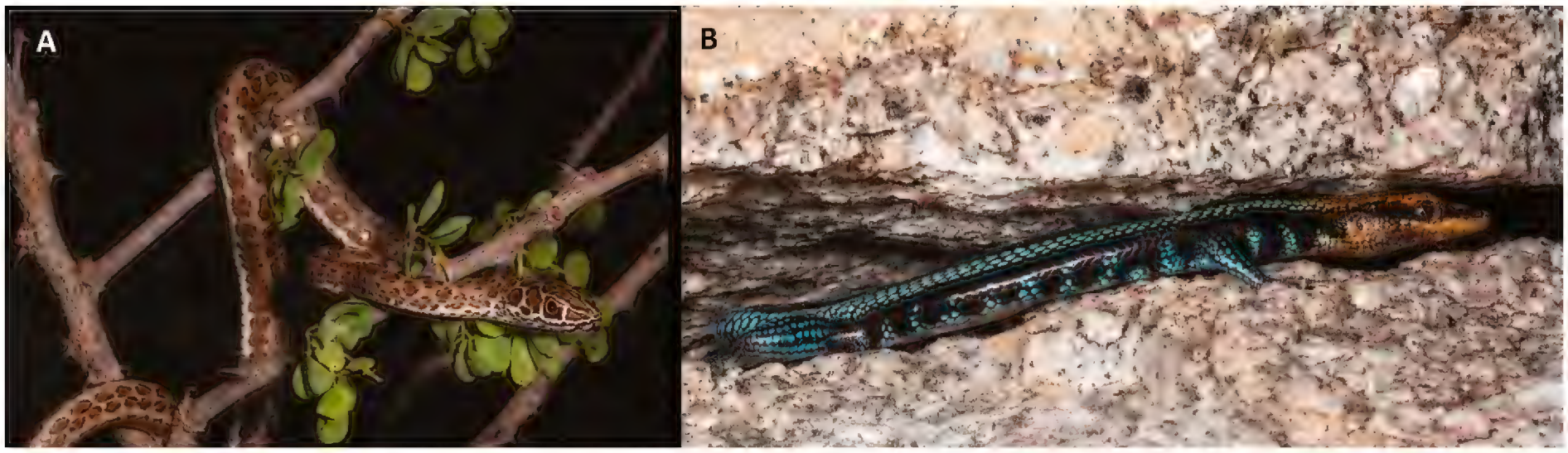

Fig. 6. **(A)** Specimen of *Psammophis leopardinus* foraging at night on a blackthorn bush at Maconjo, possibly preying on *A. ansorgii*. **(B)** First topotypic material of *Trachylepis laevis* collected in over 110 years, FKH0018 in life; note flattened body adapted to shelter among tight rocky spaces.

cryptic diversity has resulted in the genus *Phyllodactylus*, as understood for over 100 years, now being distributed among the families Diplodactylidae, Gekkonidae, and Phyllodactylidae and in at least 15 genera! It is thus not surprising that the generic affinities of *Afrogecko ansorgii* remain problematic. When initiating a major generic revision of phyllodactyline geckos, Bauer et al. (1997) provisionally assigned *ansorgii* (then known only from the types) to the genus *Afrogecko*, but noted that its affinities would need re-assessment on discovery of new material.

Subsequently Haacke (2008) described the new plume-tailed gecko from the Angolan Namib region that was again tentatively assigned as *Afrogecko plumicaudus* in the absence of genetic studies. The collection of additional new material by Wulf Haacke allowed its phylogenetic affinities to be assessed, whereupon it was transferred to a new gekkonine genus *Kolekanos* (Heinicke et al. 2014). Although all the original material was collected under thin, exfoliating rock slabs, the species was later shown to forage arboreally (Agarwal et al. 2017). In its (at least) partial arboreal behavior, *K. plumicaudus* is similar to *A. ansorgii*. Nevertheless, *A. ansorgii* is unique among southern African leaf-toed geckos, in being exclusively arboreal and by what appear to be some remarkable ecological adaptations. The morphological differences found in specimens obtained at the type locality and Sta Maria, namely in body size and number of cloacal spurs, likely reflect local adaptations and may be climatically driven. Further detailed morphological and genetic studies are ongoing to confirm the generic placement of *A. ansorgii* and explore intraspecific variation (data not shown).

Southwestern coastal Angola is subject to frequent advective fogs and relatively cool temperatures, caused by the cold offshore Benguela current, and experiences a climatic gradient of increased rainfall from the coast inland (Huntley 2019). The importance of advective fog and low clouds in shaping the local arid ecosystems has been relatively well studied in Namibia, where it has been estimated to represent up to five times the amount of precipitation provided by rain (Seeley and Henschel 1998). The frequency of this type of fog is high in coastal areas, but studies in the central Namib found the amount of precipitation to be highest around 35–60 km inland and below 500 m asl, where low strata clouds were intercepted by local elevation (Lancaster 1984). Satellite imagery show that advective fog and low clouds penetrate further inland in the southern and northern sections of the Namib (Cermak 2012), but relatively little effort has focused on the role of fog and low clouds in Angola. Nevertheless, it has been suggested that the incidence of winter fog and low strata clouds is especially pronounced between the towns of Namibe and Benguela, leading to heavy morning dew and allowing for a local abundance of epiphytic lichens (Huntley 2019). The presence of these epiphytic lichens was recorded at the site of Sta Maria, where they often almost covered the branches of blackthorn bushes. Being close to the sea shore and situated in an extensive dry valley, the collecting site at Sta Maria is subject to frequent morning coastal

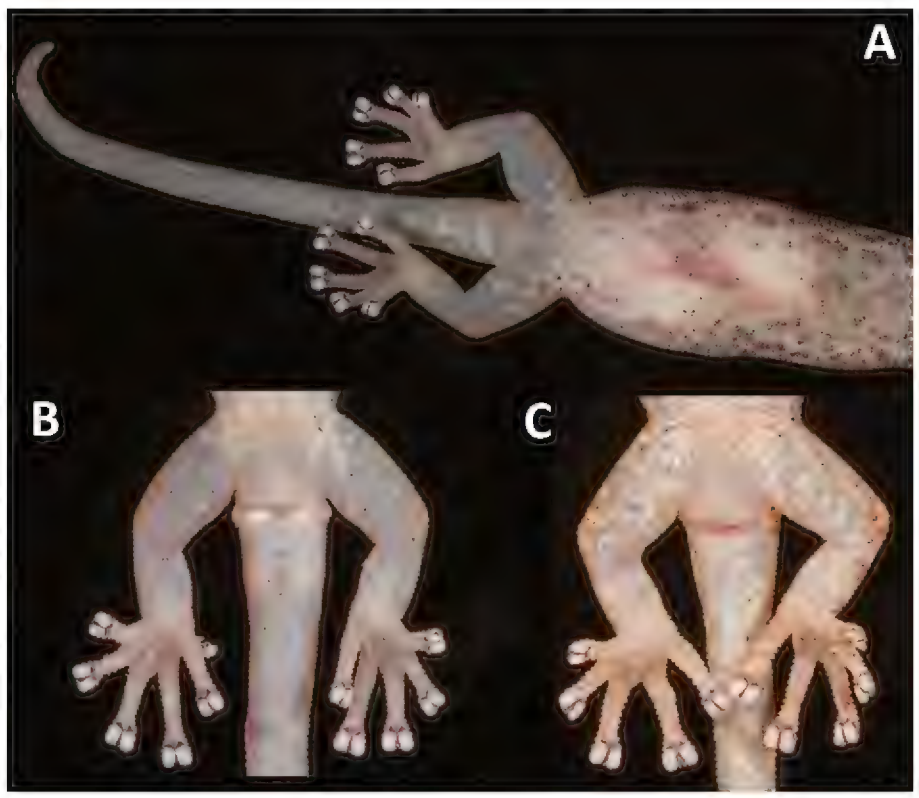

Fig. 7. **(A)** Female *Afrogecko ansorgii* from Maconjo, FKH0007, gravid with two eggs. Note enlarged precloacal scales and presence of one cloacal spur. **(B)** Cloacal region of male *A. ansorgii,* FKH0008. Note single chevron row of nine precloacal pores, hemipenial bulges (as paired light swellings) and cloacal spurs (small white tubercular scales on lateral surfaces of tail base) in the male. **(C)** Cloacal region of female *A. ansorgii*, FKH0009. Note lack of precloacal pores on the chevron row of enlarged scales or of enlarged tubercular lateral scales on tail base. Both sexes have delicate elongate toes with a single pair of terminal scansors. The cylindrical tail is finely scaled, and non-verticillate, lacking obvious lateral constrictions.

advective fogs which become trapped among high rocky slopes. Although lichens were less abundant at Maconjo, the type locality also appeared to be regularly subject to thick foggy conditions. Situated at around 40 km from the coast and 400 m asl, Maconjo lies at the base of a north-south oriented orographic step, characterized by mountainous granitic hills that elevate the coastal plateau further east to above 800 m asl, and therefore topography likely plays a role in containing fog and low strata clouds and, ultimately, shaping the ecological conditions of local spiny savannas. The blackthorn bush holds a reputation for being termite-resistant (Schmidt et al. 2002). Nevertheless, in both Maconjo and Sta Maria we found 'drywood' termites (family Kalotermitidae) to be present inside dead blackthorn branches, often leaving them neatly excavated. This was especially evident at the drier environment of Sta Maria, where large numbers of dead branches break and accumulate on the ground underneath the bush canopy, thus providing an abundance of sheltering habitat for the gecko. Drywood termites are well adapted to arid ecosystems but may also require some moisture and tend to be uncommon or patchily distributed. It appears therefore that the local distribution of termites is driven by specific environmental conditions affecting the bushes of *Senegalia mellifera detinens*, like altitude and rainfall, atmospheric moisture provided by fog or low clouds, and the frequency and severity of droughts. In regions with relatively higher moisture from average rainfall, these blackthorn savannas may not accumulate enough dead wood and the conditions might be unsuitable for the termites and ultimately the gecko. On the other hand, under extremely dry conditions the termites may not thrive, or the density of bushes might be too low, not providing enough shelter or foraging habitat for this exclusively arboreal gecko. Therefore, the dry coastal blackthorn savannas that experience low rainfall but are subject to frequent fogs, seem to constitute the 'sweet spot' habitat for the species.

Formerly known locally as *Deserto de Mossamedes*, the northernmost extension of the Namib Desert stretches north along the Atlantic coast of Angola from the Angola-Namibia border for 450 km to about the city of Benguela. Fronting the Atlantic Ocean to the west, it gradually ascends in elevation eastward to a semiarid plain dominated by acacia and mopane [African ironwood] trees that abuts the steep Serra de Chela escarpment. Characterized by gravel plains and rock platforms interspersed with sand dune fields, the Angolan Namib is part of a broader ecoregion defined as Kaokoveld Desert (Burgess 2004). It is believed that ancient climatic stability, a mosaic of substrates and incidence of coastal fogs contribute to high species richness and rates of endemism in the Namib region (Seeley et al. 1998), and the Kaokoveld is often referred to as a regional center of endemism for flora (Van Wyk and Smith 2011), beetles (Koch 1961), and lizards (Lewin et al. 2016; Branch et al. 2019b). Nevertheless, the boundaries of the northern Kaokoveld have remained poorly defined and although Burgess (2004) depicted the ecoregion along the Angolan coast to about Benguela town, other authors have set the northern limit at Lucira, in Namibe Province (e.g., Craven 2009; Branch et al. 2019). Between Lucira and Benguela the semi-arid ecosystems characterized by a diversity of succulent plants progressively gives way to semi-arid dry savannas dominated by acacia species (Barbosa 1970), thus placing our surveyed sites on the fringes of the Kaokoveld ecoregion. Historical and recent herpetological work on the Angolan arid ecosystems has mostly focused in the southernmost regions of the Angolan Kaokoveld (Marques et al. 2018; Branch et al. 2019b), and about one-third of national reptile diversity is known to occur in the Namibe Province alone, with gekkonids being the most speciose group (Ceríaco et al. 2016). In comparison, less effort has been directed to Benguela Province, yet the diversity and new extension ranges here reported suggest that the herpetological richness of the province may have been underestimated. It is likely that future surveys across the northern limits of the Kaokoveld will further increase the regional lists, unveil cryptic diversity, and underline the ecological significance of the local spiny semi-arid savannas associated with fog and low strata clouds. Apparently restricted to Benguela's Kaokoveld and strongly associated with the local fog ecosystem, the now rediscovered Ansorge's gecko remains as one of the most unique and iconic representatives of Angolan herpetofauna.

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Bill Branch (William R. Branch) was born in London, United Kingdom. He was employed as Curator of Herpetology at the Port Elizabeth Museum for over 30 years (1979–2011), and upon his retirement he was appointed Curator Emeritus Herpetology until his death in October 2018. Bill's herpetological studies concentrated mainly on the systematics, phylogenetic relationships, and conservation of African reptiles, but he has been involved in numerous other studies on the reproduction and diet of African snakes. He has published over 300 scientific articles, as well as numerous popular articles and books. The latter include: *South African Red Data Book of Reptiles and Amphibians* (1988), *Dangerous Snakes of Africa* (1995, with Steve Spawls), *Field Guide to the Reptiles of Southern Africa* (1998), *Tortoises, Terrapins and Turtles of Africa* (2008), and *Atlas and Red Data Book of the Reptiles of South Africa, Lesotho and Swaziland* (multi-authored, 2014), as well as smaller photographic guides. In 2004, he was the 4th recipient of the "Exceptional Contribution to Herpetology" award of the Herpetological Association of Africa. Bill has undertaken field work in over 16 African countries, and described nearly 50 species, including geckos, lacertids, chameleons, cordylids, tortoises, adders, and frogs.